Thiabendazole Resistance in *Fusarium* Species Associated with Dry Rot of Potato

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ABSTRACT

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The incidence of thiabendazole (TBZ) resistance in *Fusarium* spp. associated with dry rot of potato tubers was estimated during 1992 and 1993. We isolated fungi from wounds or preexisting lesions on randomly-collected seed, tablestock, and processing tuber samples, primarily from the northeastern United States. Of 154 samples, 99 yielded one or more *Fusarium* isolates, 98% of which were pathogenic on

potato tubers. The most frequently recovered pathogenic species were *F. sambucinum*, *F. solani*, and *F. oxysporum*, but pathogenic isolates of *F. acuminatum*, *F. avenaceum*, *F. crookwellense*, *F. culmorum*, and *F. equiseti* were also isolated. Significant logistic regression relationships were found between the *Fusarium* species isolated and factors such as tuber use, method of isolation, year of isolation, and state of origin of the sample. Of the 200 *Fusarium* isolates, 83 were resistant to TBZ (5 mg/L or higher); these included isolates of *F. sambucinum*, *F. solani*, *F. oxysporum*, *F. culmorum*, *F. avenaceum*, and *F. acuminatum*. TBZ-resistant isolates were obtained from most locations and all tuber types. The effective dose for fifty percent reduction in growth differed among isolates of *F. sambucinum* and *F. solani*, suggesting that there may be multiple beta-tubulin mutations which confer resistance.

Additional keywords: *Fusarium coeruleum*, *F. sulphureum*, *Gibberella pulicaris*, *Nectria haematococca*, *Solanum tuberosum*

Fusarium dry rot is a postharvest disease of potato (*Solanum tuberosum* L.) of world wide significance (10). Though comprehensive figures are lacking, average annual crop losses attributed to dry rot have been estimated at 6 - 25% (4), with reports that greater than 60% of tubers in storage can be affected (3). The greatest losses occur during long-term storage of potato tubers, after growers have incurred most of the production costs. Dry rot is readily spread among tubers during the handling and planting of tubers, and is an important cause of seed tuber rot and poor stands (10).

Fusarium dry rot is also of great importance to the consumer, as some of the *Fusarium* species that cause dry rot produce mycotoxins (2, 6, 20). One major group of mycotoxins produced are trichothecenes, which are inhibitors of eukaryotic protein

synthesis (29) and can pose serious health problems, both acute and chronic, for animals and humans (20, 29, 33).

Many species of *Fusarium* cause dry rot. The predominant causal agents are *F. solani* (Mart.) Appel & Wollenw. (10, 31) (teleomorph *Nectria haematococca* Berk. & Br.), also called *F. coeruleum* (Libert) Sacc. (21), *F. oxysporum* Schlect. emend. Snyd. & Hans. (28, 31) and *F. sambucinum* Fuckel (10) (teleomorph *Gibberella pulicaris* (Fr.) Sacc.), also called *F. sulphureum* Schlecht. (21). Other species also have been reported to cause dry rot, including *F. acuminatum* Ell.&Ev. (teleomorph *G. acuminata* Wollenw.) (27, 28, 31), *F. avenaceum* (Fr.) Sacc. (teleomorph *G. avenacea* Cook) (9, 27), *F. crookwellense* Burgess, Nelson & Toussoun (8, 31), *F. culmorum* (Smith) Sacc.(9, 27), *F. equiseti* (Corda) Sacc. (teleomorph *G. intricans* Wollenw.) (28, 31), *F. graminearum* (teleomorph *G. zeae*) (27, 31) *F. scirpi* (31), *F. semitectum* (28), *F. sporotrichioides* (27) and *F. tricinctum* (27). However, these species are usually considered to be of lesser importance.

Control of Fusarium dry rot has been accomplished primarily by postharvest applications of thiabendazole (TBZ), a benzimidazole fungicide, which is applied to tubers before storage. This is the only fungicide registered for postharvest control of dry rot in the United States. The development of fungicide resistance in several of the *Fusarium* species which cause this disease has resulted in control failures. Isolates of *F. sambucinum* which show resistance to TBZ were found, first in Europe (32), and subsequently in North America (5, 13). Hanson and Loria obtained isolates of *F. sambucinum* that were highly resistant to TBZ from tubers showing severe dry rot symptoms; these tubers were obtained from a potato storage in which TBZ had been used during 1991 (unpublished data). TBZ-resistant isolates of *F. solani* (16) and *F. culmorum* (9) have been reported in Europe, but not elsewhere.

Data on the fusaria causing dry rot and a quantitative assessment of the sensitivity of *Fusarium* populations to TBZ are needed to determine the potential

impact of fungicide resistance on dry rot control, and for development of management strategies, including fungicide recommendations. Our objective was to identify and characterize the *Fusarium* species causing dry rot of potato tubers grown or used in the northeastern United States, and to determine the prevalence of TBZ-resistance in these species. We found that eight *Fusarium* species cause potato tuber dry rot in the Northeast, and that TBZ-resistance is prevalent in *F. sambucinum* and present in five *Fusarium* species.

MATERIALS AND METHODS

Isolate Collection. Potato tubers were collected from cooperators throughout the northeastern United States. Tubers were collected without regard to Fusarium dry rot symptoms, to obtain an unbiased estimate of the frequency of TBZ resistant isolates in the *Fusarium* population associated with commercially produced tubers in the northeastern United States. A total of 154 samples of 10 - 20 tubers each was obtained from throughout the Northeast. Tubers produced for seed, tablestock and processing were included among the samples. Data on location, seed source, potato cultivar and symptom development were catalogued.

Up to six tubers with existing lesions were randomly selected from each sample. Fungi were isolated by plating necrotic tissue excised from the edge of lesions in interior tuber tissues onto 2 % water agar (WA) amended with streptomycin (300 mg/L) and penicillin G (100 mg/L). Isolates were transferred to WA and V8 agar plates for short-term storage. Isolates were grown on V8 agar slants for 4-5 days and stored at 4 C. Isolates were also grown on WA plates overlaid with sterile glass fiber filter paper squares. Once the fungus had grown beyond the filter paper (5-8 days), papers were

peeled from the agar, placed in sterile paper coin envelopes, and dried in a closed plastic container with anhydrous $CaSO_4$ and stored at -20 C (23).

Tubers free of symptoms were wounded, using two methods, to bait for fusaria (30). Tubers were separated into two groups. One group was cut in half with a sterile knife and shaken in a paper bag for approximately 10 seconds in any soil carried with the initial sample. The other group was bruised by dropping from a height of 1.5 meters onto a cement floor that had been surface disinfested with 10% Clorox (0.525% sodium hypochlorite). Tubers were placed in paper bags and incubated at 24-28 C for 1-2 weeks and examined for lesions. Isolates were obtained from lesions that developed from wounds, as described previously.

Isolate Characterization. The species of each *Fusarium* isolate was determined using techniques described by Nelson et al. (21). Isolates were single-spored and transferred onto potato dextrose agar slants (21) to check pigment production, and onto carnation leaf agar (21) for sporulation. Cultures were examined weekly for up to 4 weeks for pigment production and spores.

Pathogenicity tests were conducted on disease-free potato tubers, (cv. Sebago). Tubers were surface disinfested for 15 min. in 10% Clorox and rinsed twice in sterile distilled water. Tubers were cut in half with a sterile knife and one cut surface was pressed for 30 seconds onto a petri plate on which a *Fusarium* isolate had grown to a colony diameter of 90-100 cm. The cut surfaces of the tubers were placed together, loosely held together with tape, incubated at 22-26 C for one week, then examined for symptoms. Control tubers were pressed onto plates of sterile water agar or a non-pathogenic *F. oxysporum* isolate for negative controls, and onto a culture of a known pathogen as a positive control. Isolates producing lesions on tuber surfaces after two weeks were considered pathogenic. Isolations were made from tubers inoculated with each species to confirm the presence of *Fusarium* in lesions. Two tubers were inoculated per isolate in each of two experiments.

TBZ sensitivity of pathogenic isolates was determined using a radial growth assay. Technical grade TBZ (Sigma, St. Louis, MO) was dissolved in ethanol and added to molten V8 agar to give TBZ concentrations of 0, 5, 10, 25 and 50 mg/L and an ethanol concentration of 1%. A plug of mycelium from the edge of a rapidly growing culture was placed on plates and incubated at 22-26 C for 5 days. Three replicate plates were used at each concentration for each isolate. Colony diameter on fungicide-amended and control plates was measured and compared. Any visible growth away from the agar plug at 5 mg/L TBZ or higher was interpreted as resistance, since sensitive isolates showed no growth at this level of TBZ. Effective dose for 50% reduction in growth (ED_{50}) was estimated from the slope of the dose response curve for each isolate. The growth rate for each isolate was determined on control plates (V8 agar with 1% ethanol). At 5 days, the colony diameter, minus the diameter of the agar plug, was determined as an average of three plates for each isolate and divided by the number of days, to give average growth rate.

Statistical analyses. Logistic regression (11) was used to analyze the data from the isolates to identify predictor variables strongly associated with TBZ-resistance and TBZ-sensitivity, a binary response.

To investigate the factors associated with TBZ-sensitivity, the samples in which infection occurred were used as the data. In the multiple logistic regression model, the probability that an isolate from an infected tuber will be TBZ-resistant depends on the values of p predictor variables. For the i^{th} isolate, these predictor variables have the values $x_i = (x_{i1},x_{i2},...,x_{ip})$, and the logit term

$$g(x_i) = \beta_0 + \beta_1 x_1 + ... + \beta_p x_p.$$

is determined by the predictor values and the coefficients β_k. The probability that an isolate with predictors equal to x_i will be TBZ-resistant is given in the logistic regression model by

$$p(x_i) = \exp[g(x_i)] / \{1 + \exp[g(x_i)]\},$$

where exp(a) denotes the exponential function e^a. The unknown coefficients β_k are estimated from the data, as are the probabilities $p(x_i)$.

The data for the i^{th} infected isolate consists of the response Y_i, which is TBZ-resistant (coded as 1) or TBZ-sensitive (coded as 0), and this isolate's values for a set of possible predictor variables. The possible predictors examined were indicator variables representing the isolate species (*F. sambucinum, F. solani,* or *F. oxysporum*), tuber use (seed, tablestock, or processing), the state of origin (NY, ME, PA, or other), the method of isolation (existing lesion or wound), year (1992 or 1993), and two-factor interactions of these.

The goal of the logistic regression analysis was to determine which predictors were significantly associated with the presence or absence of TBZ resistance. Best subsets (also known as all-possible-subsets) regression (11) was used to find good models containing one predictor, two predictors, etc., which were examined individually in detail. Two kinds of models were considered: models containing only main effects, and models including two-factor interactions as well as main effects. The computer analysis was performed using the procedure LOGISTIC in the SAS statistical computing language (25, 26).

The goodness of fit of models derived from logistic regression was assessed by using log likelihood (LL) statistics (11). The test statistic for overall significance of a model M was

$$G = G(M) = -2[LL(C) - LL(M)],$$

where C denotes the constant-only model, which contains an intercept but has zero coefficients for all predictors. Under the null hypothesis that all predictor coefficients are 0, G has a chi-square distribution with p degrees of freedom, where p is the number of predictors in model M. The significance of improvement of model M over a reduced (smaller) model M', containing p' of the p predictors in M, was tested by computing

$G_{difference} = G(M)-G(M')= -2[LL(M') - LL(M)]$.

Under the null hypothesis that the coefficients of all predictors in model M but not in M' are 0, this G has a chi-square distribution with p-p' degrees of freedom. A model or model improvement was considered statistically significant if the corresponding G attains the 0.05 level of statistical significance.

Classification tables were used to supplement the log likelihood measures of model fit. The observed responses were cross-classified with the responses predicted by the estimated model. Good predictive accuracy, i.e., a high proportion of responses correctly predicted, constitutes evidence that prediction of response based on the logistic regression model gives improved results over prediction of response without this model. (Because classification tables reduce the estimates of the $p(x_i)$, a continuous measure of outcome, to a binary prediction of outcome, losing information that is present in the data, and because classification accuracy is influenced by the relative numbers of responses of the two kinds (1's and 0's), the log likelihood tests were used as the primary analyses, supplemented by the classification tables.)

The same logistic regression approach was used to examine the factors associated with infection of tubers by *F. sambucinum*, *F. solani*, and *F. oxysporum*. The number of tubers infected by each species was small (69, 44, and 58 cases out of 1540, respectively). Each species was analyzed separately, as different factors may influence the infection process for the three species. In the first of these analyses, the response variable was either "infected by *F. sambucinum*" (coded as 1) or "not infected by *F. sambucinum*" (coded as 0); the other two species were analyzed the same way. The factors considered were tuber use, state, method of isolation, and year. Again, both main effect models and interaction models were examined to determine significant associations of these factors with infection.

RESULTS

Of the154 tuber samples obtained, 99 yielded one or more *Fusarium* isolates, for a total of 200 isolates. The samples included tubers intended for use as seed (85 samples), tablestock (43 samples) and processing (26 samples). Most of the samples were procured from New York (75 samples), Maine (51 samples) and Pennsylvania (19 samples) (Fig. 1). However, tubers were also collected from New Jersey and Connecticut. Some seed samples came from tuber lots which were grown in other states (Michigan, Nebraska, and South Dakota) or a Canadian province (New Brunswick) and shipped to the Northeast. Most of the seed samples were obtained from New York and Maine (Fig. 1). Thirty five (23%) of the tuber samples had been treated with a benzimidazole fungicide. Fourteen (9%) of the samples were from tuber lots with economically significant levels of dry rot, based on documentation received from growers.

Eight *Fusarium* species were isolated (Fig. 2). *Fusarium sambucinum*, *F. oxysporum* and *F. solani* were the most common species, comprising 35.5%, 28%, and 22% of the isolates, respectively, and were widely distributed (Fig. 2A). *F. avenaceum* and *F. culmorum* were less common, comprising approximately 7.5% and 5% of the isolates, respectively. The other species were infrequent: *F. equiseti* (1%), *F. acuminatum* (0.5%), and *F. crookwellense* (0.5%). *F. sambucinum*, *F. solani, F. oxysporum, F. avenaceum*, and *F. culmorum*, were found in all tuber types (Fig. 2B). The infrequent species were found only in the tablestock and processing samples (Fig. 2B).

One hundred sixty isolates were obtained from pre-existing lesions. These included all eight of the species identified, *F. sambucinum* (41%), *F. oxysporum* (20%), *F. solani* (22%), *F. avenaceum* (8.5%), *F. culmorum* (6%), *F. acuminatum* (0.7%), *F.*

crookwellense (0.7%), and *F. equiseti* (0.7%). Thirty-eight percent of the isolates obtained from pre-existing lesions were resistant to TBZ.

Forty of the 200 isolates were obtained from wounded potatoes. These included six of the eight species identified, *F. solani* (37.5%), *F. oxysporum* (35%), *F. sambucinum* (17.5%), *F. avenaceum* (5%) and one isolate each of *F. culmorum* and *F. equiseti*. Both TBZ-sensitive and TBZ-resistant isolates were obtained, a total of eight TBZ-resistant isolates were obtained from wounded tubers (20% of the isolates). No significant differences were found between the proportions of *Fusarium* species recovered from bruised and cut tubers (P=0.86).

The models that showed a significant logistic regression relationship between predictors and infection differed markedly among the three species. For *F. sambucinum*, the only significant main effect model was the one with method of isolation as the sole predictor (G=41.07, p =0.0001, Table 1). Thus *F. sambucinum* was significantly less common from wounded potatoes than from existing lesions. This model was not improved significantly by adding any other main effect predictors. Among interaction models, this model remained the best with a single predictor; however, significantly improved models were obtained by adding one or two interaction predictors, as shown in Table 1. The interaction predictors that appeared most frequently in these models were interactions of tuber use and state.

For *F. solani*, significant main effect models with one to three predictors were found. The most commonly appearing predictors were indicators of tuber use (seed, tablestock). However, indicators of state, year, and method of isolation were also present in the models shown in Table 2. Significant interaction models with one to three predictors were also found. For two and three predictors, the best fitting interactions models have higher G values than the best fitting main effect models (Table 2) Among the best interaction models, the most commonly occurring interaction term is that of the state of Pennsylvania with the method of isolation.

For *F. oxysporum*, the most highly significant single-predictor main effect model was based on the indicator of the state Pennsylvania. Significantly improved models containing two or three predictors were obtained by adding indicators for method, year, tuber use (tablestock), and other states as shown in Table 3. Interaction models as a group do not perform better than main effect models; as Table 3 shows, the one- and three-predictor models with the highest G values contain only main effects. Among two-predictor models, the two-predictor model with the highest G contains only one interaction term, the interaction of method and year, and the model with the second-highest G is the main effect model.

Of the 200 *Fusarium* isolates obtained, 83 were resistant to TBZ at 5 mg/L. Resistant isolates were obtained from all locations and from all tuber types. The proportion of TBZ-resistant isolates varied greatly by species (Fig. 3). The majority of the resistant isolates were *F. sambucinum* (67 isolates). The remainder of the resistant isolates were *F. solani* (8 isolates), *F. oxysporum* (5 isolates), *F. acuminatum* (1 isolate), *F. avenaceum* (1 isolate) or *F. culmorum* (1 isolate).

Several models were found that showed a highly significant logistic regression relationship between predictors and TBZ sensitivity. Among main effect models, the predictor with the strongest effect was the indicator of whether the infecting species was *F. sambucinum*. The model with this as the sole predictor was significant ($G=141.79$, $p=0.0001$). A few main effect models containing this predictor and one or two additional predictors were significant improvements on the single-predictor model, as shown in Table 4. All of the models listed in Table 4 demonstrate the presence of strong associations between TBZ-sensitivity and predictor variables based on species, state, and year. However, the most powerful predictor, both by itself and in combination with others, is the indicator for *F. sambucinum*. Predictors that appeared in many of these models were the indicators for Maine and for Pennsylvania. Among models that include interaction terms as well as main effects, the model based on the

interaction of *F. sambucinum* and year (1992 or 1993) had a slightly higher G value (G=144.89, p=0.0001) than the main effect model based on *F. sambucinum* alone. However, this interaction did not appear in any of the best two- and three-predictor models. Improved models containing this and one or two additional predictors are shown in Table 4. The interaction predictor that appeared most frequently was the indicator for *F. solani* in Maine.

According to the best main effect single-predictor model, all *F. sambucinum* are predicted to be TBZ-resistant, and all other species are predicted to be TBZ-sensitive. The correct prediction rate among those isolates observed to be TBZ-resistant is 85/(85+2) = 97.7%; the correct prediction rate among those isolates observed to be TBZ-sensitive is 67/(67+11) = 85.9%. All models have very high correct prediction rates, but these should be interpreted with caution, as they are all based on the very strong relationship between TBZ-resistance and *F. sambucinum*.

These results were obtained from analyses that excluded the few (29) observed cases of isolates infected by species other than *F. sambucinum, F. solani, and F. oxysporum*. When the reported analyses were performed again, with these 29 cases present, amalgamated as a fourth species category, the results differed only in minor details.

Resistant *F. sambucinum* isolates, those that grew at 5 mg/L or above, clustered into three categories, based on radial growth at 5 mg/L relative to the unamended control (Fig. 4). These groups corresponded to ED_{50} levels of high (ED_{50} >30 mg/L), medium (ED_{50} 8-20 mg/L), and low (ED_{50}<5 mg/L). Most of the *F. sambucinum* isolates (57) had a high level of TBZ resistance. However, four isolates had a moderate level of resistance, and six isolates had a low level (Fig 4). *F. solani* isolates were variable in their dose response to TBZ (Fig. 5), two with a high level of TBZ resistance (ED_{50} >30 mg/L), and six with a low level of resistance (ED_{50}<5 mg/L). All of the other

TBZ-resistant *Fusarium* species (*F. acuminatum*, *F. avenaceum*, *F. culmorum*, and *F. oxysporum*) had a low level of resistance (ED_{50}<5 mg/L).

Ninety eight percent of the isolates were pathogenic on cut potato tubers. This included all eight species isolated, and all TBZ-resistance categories of *F. sambucinum*. The three nonpathogenic isolates included two TBZ-sensitive *F. oxysporum* isolates and one *F. sambucinum* isolate with a low level of TBZ-resistance.

Growth of TBZ-resistant isolates of *F. sambucinum* and *F. oxysporum* was not significantly different from growth TBZ-sensitive isolates (P=0.76 and P=0.97 respectively). However, the average growth rate of TBZ-resistant isolates of *F. solani* was less than that of TBZ-sensitive isolates (probability of being equal, P=0.035), and one had malformed hyphae and spores.

DISCUSSION

Forty-two percent of the isolates in our study were resistant to TBZ. The majority of the resistant isolates we identified were *F. sambucinum*. The proportion of *F. sambucinum* isolates resistant to TBZ (97%) is consistent with the results of a study conducted in the United States by Desjardins et al. (5). In that study, 24/25 (96%) of the *F. sambucinum* isolates collected from dry rot lesions during 1990 and 1991 were resistant to TBZ (5). However, other dry rot-causing fusaria were not included in this study. The proportion of TBZ-resistant *F. sambucinum* isolates found in the United Kingdom (68%) (9) and in Canada (60%) (13) were lower than reports from the United States.

We also identified TBZ-resistant isolates of *F. acuminatum*, *F. avenaceum*, *F. culmorum*, *F. oxysporum*, and *F. solani*. Resistance has been reported in *F. solani* (16) and *F. culmorum* (9) isolates from potato in Europe, but this is the first report of

TBZ resistance in these species in North America. Benzimidazole-resistance has been reported in isolates of *F. oxysporum* recovered from other hosts (7), but not previously in isolates from potato. This is the first report of TBZ-resistance in *F. acuminatum* and *F. avenaceum* from potato.

The level of resistance to TBZ (ED_{50} >30 mg/L) of most of the *F. sambucinum* isolates in this study was similar to that found in other studies (ED_{50} 30-40 mg/L) (5, 9, 32). However, we found four isolates with a moderate ED_{50} (10-20 mg/L), and six isolates with a low ED_{50} (<5 mg/L). Four of the low ED_{50} isolates produced a red pigment, similar in color to the pigment produced by *F. avenaceum* and *F. culmorum*, while the other TBZ-resistant *F. sambucinum* isolates did not produce a red pigment. One of these red *F. sambucinum* isolates was non-pathogenic on potato tubers, while all other *F. sambucinum* isolates were pathogenic. The level of resistance to TBZ in *F. solani* also varied among isolates. In other filamentous fungi, benzimidazole-resistance levels have been found to correspond to specific mutations in the beta-tubulin gene (14, 15). Differences in TBZ sensitivities of isolates within species, as indicated by ED_{50} values, suggests that TBZ resistance in *Fusarium* may also be conferred by more than one mutation in that gene.

There is no evidence for reduced growth or pathogenicity in TBZ-resistant isolates of *F. sambucinum* or *F. oxysporum*. This is consistent with previous reports (5, 9, 13), and suggests that control of Fusarium dry rot of potato with postharvest TBZ applications will be compromised. The slow growth rate of the TBZ-resistant *F. solani* isolates in culture, relative to the TBZ-sensitive isolates of *F. solani*, suggests that in this species, there may be some fitness costs associated with TBZ-resistance. However, all of the TBZ-resistant *F. solani* isolates were pathogenic on potato tubers.

The high proportion (56%) of TBZ-resistant isolates recovered from tubers produced for seed suggests that dry rot may be more difficult to control in the future. *Fusarium* spp. have been shown to spread to new tubers from infected seed tubers (1,

17, 18). The prevalence of TBZ-resistant isolates in seed could be of particular concern since there is a potential for increased rot severity in seed tubers when tuber lots with TBZ-resistant isolates are treated with TBZ, compared to tubers not treated with TBZ (22).

F. sambucinum isolates were more frequent in pre-existing lesions than in wounds created for the purposes of this study. Pre-existing lesions were the result of tuber injury during harvest and postharvest handling. We wounded tubers two to three months after harvest. Differences in *F. sambucinum* frequency may be due to poor survival of this fungus in the soil with the tubers or on tuber surfaces. Other researchers have reported lack of evidence for long term survival of *F. sambucinum* in soil (17).

Previously, *F. solani* was identified as the most frequent and aggressive seed tuber pathogen in the United States, though *F. sambucinum* was also frequently isolated (10). We also found these species to be frequent in seed, as well as other stored tubers. Worldwide, twelve species of *Fusarium* have been reported to cause dry rot (8, 9, 10, 27, 28, 31). We found eight of these species in the Northeast.

The logistic regression models demonstrate associations between tuber infection by *F. oxysporum, F. sambucinum*, and *F. solani,* and predictor variables based on state, tuber use, isolation method, and year. However, the prediction accuracy of these models was not high (not substantially greater than 50% in both categories), in large part because of the small number of infected tubers. However, the p-values of 0.0001 for G of these models show that the models are significant. All of the models show that associations are present; determination of the precise nature of those associations would require further data and analysis.

Fusaria infect potato tubers through wounds (24), which occur at harvest or during handling. Minimizing tuber injury at harvest and providing storage conditions that promote rapid wound healing immediately after handling are important control

strategies. However, stony soils or poor weather conditions during the growing season or at harvest greatly limit the effectiveness of this strategy. Dry growing seasons increase the specific gravity of tubers, making them more susceptible to bruising. Dry soil conditions at harvest reduce the quantity of soil carried onto the primary chain of the digger, thus reducing cushioning of the tubers and increasing bruising. Infection can be limited to some degree by managing storage temperatures and humidity immediately after harvest, however, temperature and humidity control is poor in many potato storages. No Fusarium dry rot resistant cultivars are available (19) and Huaman et al. suggest that resistance to different species of *Fusarium* may be genetically independent (12), which would make the development of resistant cultivars difficult. Thus the development of fungicide resistance in *Fusarium* is of great concern in the management of dry rot, and alternative control practices are needed.

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Table 1: Best logistic regression models for predicting infection of tubers with *Fusarium sambucinum* from state, tuber use, isolation method, and year.

G of model[a]	Model type[b]	Predictors[c]
One-predictor models		
41.07	M	Method
29.46		Method*Year
21.43		U:seed*Method
16.86		S:NY*Method
Two-predictor models[d]		
49.41		Method, S:NY*U:T
48.15		Method, S:ME*U:T
45.31		Method, S:ME*U:seed
Three-predictor models[e]		
55.32		Method, S:ME*U:seed, S:NY*U:T
55.23		Method, S:ME*U:T, S:NY*U:T
54.95		Method, S:ME*U:T, S:NY*U:seed

[a]For all models in table, the P-value corresponding to G is .0001

[b]For model type, M = main effects model, blank = interactions model

[c]Predictor notation:

Indicators for states are S:NY, S:ME, and S:PA

Indicators for use categories are U:seed, U:T=tablestock, and U:P=processing

Indicator distinguishing existing lesion from wound is Method

Indicator distinguishing 1992 from 1993 is Year

Interactions are denoted by *

[d]Two-predictor models listed are those showing significantly improved fit over the Method one-predictor model, as measured by G for model comparison.

[e]Three-predictor models listed are those showing significantly improved fit over the best two-predictor model based on their predictors, as measured by G for model comparison.

Table 2: Best logistic regression models for predicting infection of tubers with *Fusarium solani* from state, tuber use, isolation method, and year.

G of model[a]	Model type[b]	Predictors[c]
One-predictor models		
17.06	M	U:seed
16.78		U:T*Year
15.80		S:PA*Method
14.16	M	U:T
Two-predictor models[d]		
30.75		Method, S:PA*Method
29.41		S:PA*Method, U:T*Year
25.36		U:seed, S:PA*Method
24.95		S:PA*Method, Method*Year
20.45	M	U:seed, S:ME
20.41	M	U:seed, Method
20.34	M	S:ME, Year
Three-predictor models[e]		
39.04		Method, U:seed, S:PA*Method
37.24		Method, S:PA*Method, S:NY*Year
36.60		Method, S:PA*Method, U:T*Year
35.80		S:PA*Method, S:NY*Method, S:NY*Year
25.47	M	U:seed, S:ME, Year
24.42	M	Method, S:ME, Year

1	23.96	M	Method, U:seed, Year
2	23.47	M	U:T, S:ME, Year

3 [a]For all models in table, the P-value corresponding to G is .0001, except P-value is
4 .0002 for G = 14.16, U:T one-predictor model.
5 [b]For model type, M = main effects model, blank = interactions model
6 [c]Predictor notation:
7 Indicators for states are S:NY, S:ME, and S:PA
8 Indicators for use categories are U:seed, U:T=tablestock, and U:P=processing
9 Indicator distinguishing existing lesion from wound is Method
10 Indicator distinguishing 1992 from 1993 is Year
11 Interactions are denoted by *
12 [d]Two-predictor models listed are those showing significantly improved fit over the best
13 one-predictor model based on their predictors, as measured by G for model comparison.
14 The two models including U:seed do not quite satisfy this condition, but are included
15 for completeness.
16 [e]Three-predictor models listed are those showing significantly improved fit over the
17 best two-predictor model based on their predictors, as measured by G for model
18 comparison.

Table 3: Best logistic regression models for predicting infection of isolates with *Fusarium oxysporum* from state, tuber use, isolation method, and Year.

G of model[a]	Model type[b]	Predictors[c]
One-predictor models		
47.55	M	S:PA
39.90		S:PA*U:T
Two-predictor models[d]		
60.48		S:PA, U:seed*Method
58.83	M	S:PA, Year
58.60	M	S:PA, Method
54.26		S:PA, S:NY*Method
53.89		S:PA, Method*Year
53.42		S:PA, S:NY*Year
Three-predictor models[e]		
71.00	M	S:PA, Method, Year
68.65		S:PA, Year, Method*Year
67.39		S:PA, S:NY*Method, S:NY*Year
64.73		S:PA, Method, S:NY*Year
62.91		S:PA, Method, U:T*Year
62.00	M	S:PA, Method, U:T

[a]For all models in table, the P-value corresponding to G is .0001

[b]For model type, M = main effects model, blank = interactions model

[c]Predictor notation:

Indicators for states are S:NY, S:ME, and S:PA

Indicators for use categories are U:seed, U:T=tablestock, and U:P=processing

Indicator distinguishing existing lesion from wound is Method

Indicator distinguishing 1992 from 1993 is Year

Interactions are denoted by *

[d]Two-predictor models listed are those showing significantly improved fit over the best one-predictor model based on their predictors, as measured by G for model comparison.

[e]Three-predictor models listed are those showing significantly improved fit over the best two-predictor model based on their predictors, as measured by G for model comparison.

Table 4: Best logistic regression models for predicting TBZ-sensitivity from species, state, tuber use, isolation method, and year.

G of Model[a]	Model type[b]	Predictors[c]	Prediction accuracy[d] Resistant	Sensitive
One-Predictor Models				
141.79	M	SA	.977	.859
144.89		SA*Year	.977	.859
Two-Predictor Models[e]				
156.54		SA, S:ME*U:T	.966	.910
152.13	M	SA, S:ME	.977	.859
150.46	M	SA, S:PA	.977	.859
149.23		SA, SO*S:ME	.954	.897
Three-Predictor Models[f]				
156.28	M	SA, S:NY, S:ME	.977	.859
156.18	M	SA, S:ME, S:PA	.977	.859
156.10	M	SA, S:PA, Year	.977	.859
155.36		SA, S:PA, SO*S:ME	.954	.897
153.26		SA,SO*S:ME, S:NY*Year	.954	.897

[a]For all models in table, the P-value corresponding to G is .0001

[b]For model type, M = main effects model, blank = interactions model

[c]Predictor notation:

Indicators for species are SA=*F. sambucinum*, SO=*F. solani*, OX=*F. oxysporum*

Indicators for states are S:NY, S:ME, and S:PA

Indicators for use categories are U:seed, U:T=tablestock, and U:P=processing

Indicator distinguishing existing lesion from wounded is Method

Indicator distinguishing 1992 from 1993 is Year

Interactions are denoted by *

[d]Prediction Accuracy values are the proportions of TBZ-resistant and TBZ-sensitive isolate infections classified correctly by logistic regression model with predictors shown.

[e]Two-predictor models listed are those showing significantly improved fit over the SA one-predictor model, as measured by G for model comparison.

[f]Three-predictor models listed are those showing significantly improved fit over the best two-predictor model based on their predictors, as measured by G for model comparison.

Figure 1: Distribution of potato tuber samples by state of origin and tuber type. The seed tuber samples included in the "other" category were collected in the Northeast, but produced in Michigan, Nebraska, New Brunswick, or South Dakota. Tablestock and processing tuber samples in the "other" category were collected from Connecticut or New Jersey.

Figure 2. A: Distribution of *Fusarium* spp. by state of origin of the sample. The "other" category includes Connecticut, New Jersey Michigan, Nebraska, New Brunswick, or South Dakota. B. Distribution of *Fusarium* spp. by tuber type. AV=*F. avenaceum*, CU=*F. culmorum*, AC=*F. acuminatum*, OX=*F. oxysporum*, SA=*F. sambucinum*, SO=*F. solani*, EQ=*F. equiseti*, and CR=*F. crookwellense*.

Figure 3. Distribution of thiabendazole (TBZ) resistant and sensitive isolates by *Fusarium* spp. AV=*F. avenaceum*, CU=*F. culmorum*, AC=*F. acuminatum*, OX=*F. oxysporum*, SA=*F. sambucinum*, SO=*F. solani*, EQ=*F. equiseti*, and CR=*F. crookwellense*.

Figure 4. Frequency distribution of *Fusarium sambucinum* isolates based on radial growth on 5 mg/L TBZ relative to growth on unamended control. Resistance categories are low growth (10-25% of control), moderate growth (50-55% of control), and high growth (70-110% of control).

Figure 5. Radial growth, as percent of unamended control, of *Fusarium solani* isolates in response to increasing thiabendazole concentrations. Each line is an average of three replicate plates of an individual isolate.

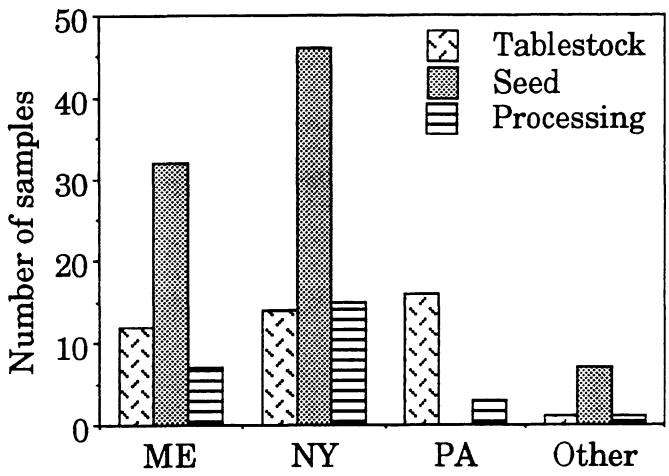
50
40
30
20
10
0
Number of samples
Tablestock
Seed
Processing
ME
NY
PA
Other

Figure 1

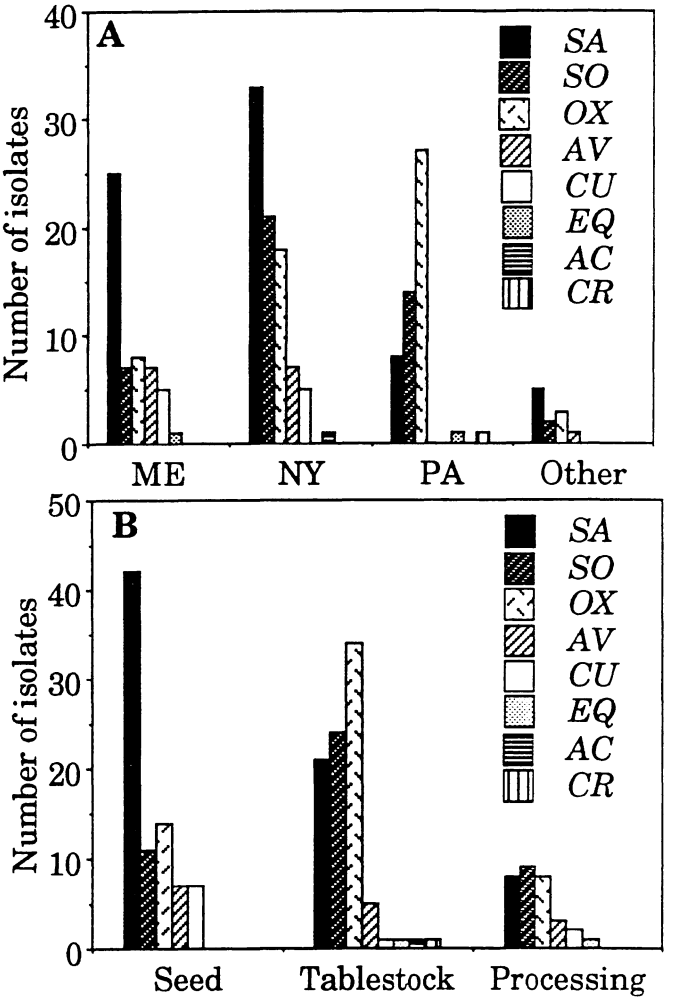
A
Number of isolates
40
30
20
10
0
ME
NY
PA
Other
SA
SO
OX
AV
CU
EQ
AC
CR
B
Number of isolates
50
40
30
20
10
0
Seed
Tablestock
Processing
SA
SO
OX
AV
CU
EQ
AC
CR

Figure 2

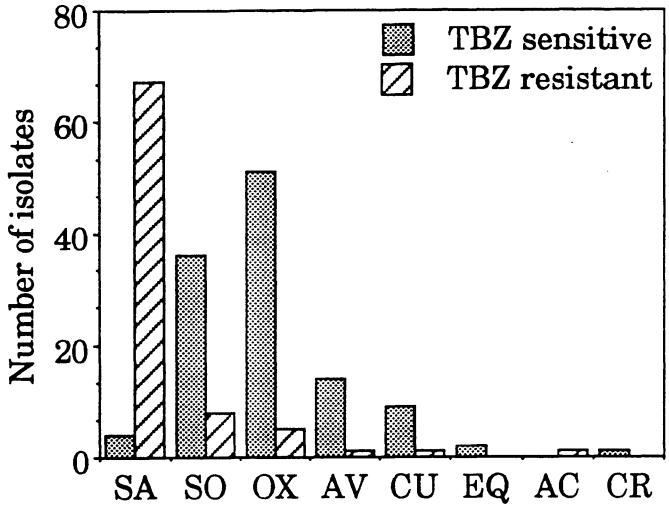
80
60
40
20
0
Number of isolates
TBZ sensitive
TBZ resistant
SA
SO
OX
AV
CU
EQ
AC
CR

Figure 3

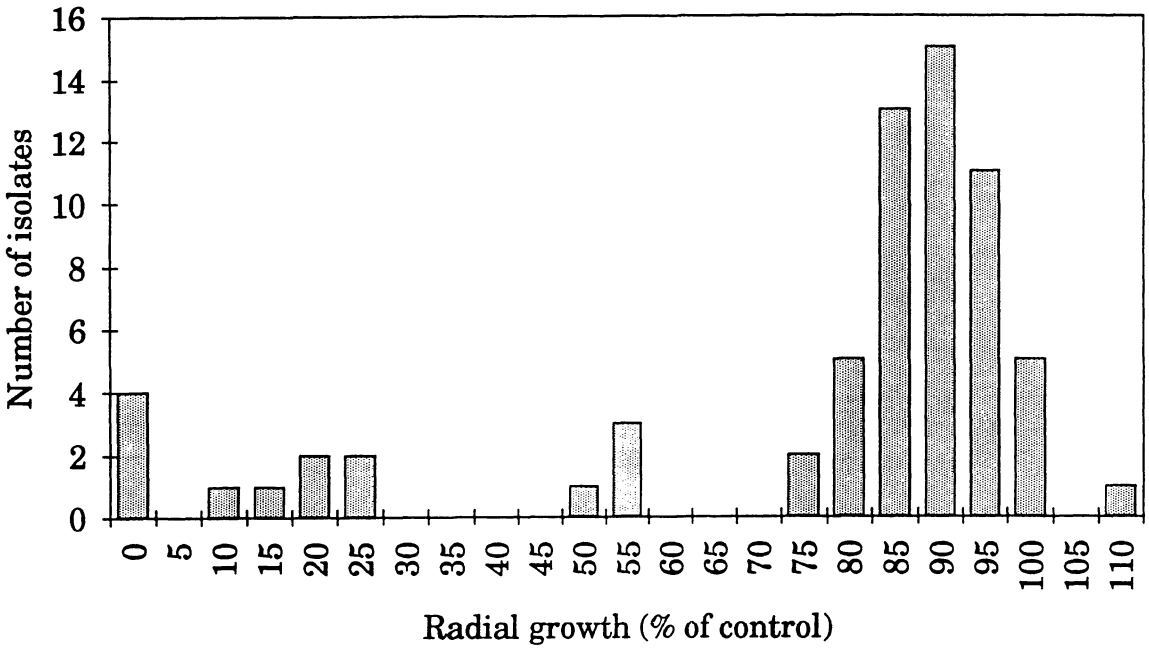
Number of isolates
16
14
12
10
8
6
4
2
0
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
105
110
Radial growth (% of control)

Figure 4

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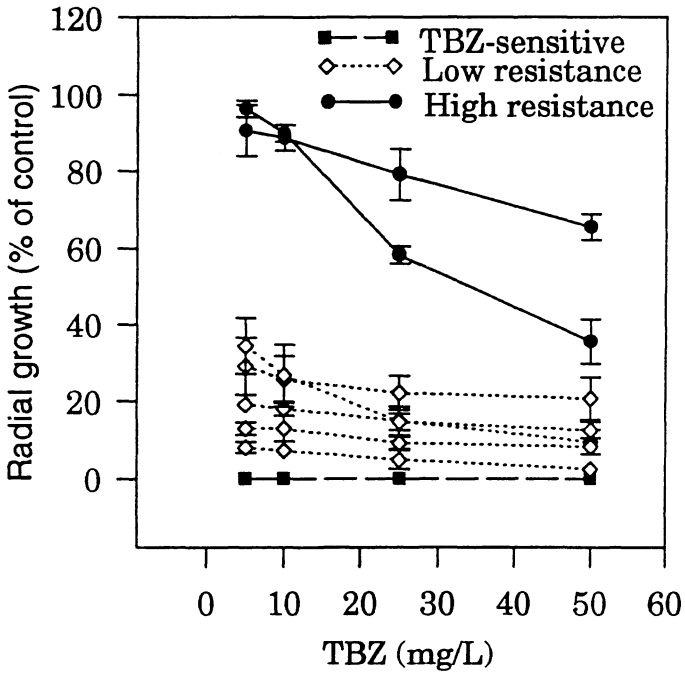

Figure 5